Forest Ecology and Management 281 (2012) 163–176

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Landscape-scale variation in structure and biomass of Amazonian seasonally flooded and unflooded forests

Joseph E. Hawes [a,*], Carlos A. Peres [a], Louise B. Riley [a], Laura L. Hess [b]

[a] School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK
[b] Earth Research Institute, University of California, Santa Barbara 93106, USA

ARTICLE INFO

Article history:
Received 26 March 2012
Received in revised form 4 June 2012
Accepted 7 June 2012
Available online 25 July 2012

Keywords:
Aboveground biomass
Brazil
Carbon stocks
Floodplain forest
Várzea
Wood specific gravity

ABSTRACT

Accurate estimates of current forest carbon stocks are required for efforts to reduce emissions from tropical deforestation and forest degradation. The relative contributions of different vegetation types to carbon stocks and potential emissions are poorly understood in highly heterogeneous forest mosaics, and further field-based measurements are necessary from severely undersampled regions and forest types to improve regional scale extrapolations based on remote sensing. We assessed the aboveground biomass (AGB) of two contiguous western Brazilian Amazonian protected areas totalling 886,176 ha, which contain vast expanses of seasonally flooded *várzea* (VZ) forest along the floodplain of the Juruá river and adjacent *terra firme* (TF) forest farther inland. Estimates were based on equations incorporating wood specific gravity (WSG) and tree height in addition to DBH, and derived from a network of 200 forest plots of 0.1 ha (=20 ha) sampled across adjacent areas of flooded and unflooded forest. A large number of small plots stratified by forest type allowed a more representative sample, encompassing the considerable variation in forest structure and composition both within and between forest types. Mean basal area per plot was higher in *várzea* forest plots than in *terra firme* plots (VZ: 37.6 ± 1.2 m^2 ha^{-1}; TF: 32.4 ± 0.9 m^2 ha^{-1}) but AGB was lower in *várzea* (VZ: 281.9 ± 12.0 Mg ha^{-1}; TF: 358.4 ± 14.4 Mg ha^{-1}) due to lower WSG and tree height. Linear mixed effects models showed the overriding effect of forest type on AGB, and the roles of water stress and a historical signature of selective logging pressure, particularly within *várzea* forests. ALOS ScanSAR generated categories of flood duration provided a more relevant description of water stress than SRTM elevation data; AGB within *várzea* forest was higher in plots subjected to longer flood duration. *Várzea* forests store significant levels of forest carbon despite their lighter-wooded trees and lower canopy stature, and yet are heavily settled by rural Amazonians, and are increasingly vulnerable to deforestation and logging. This study helps understand how baseline environmental gradients and human disturbances in these unique forests affect their carbon storage value, and highlights their importance both within and outside existing protected areas.

1. Introduction

Amazonian forests are of utmost importance in the global carbon balance representing both a substantial source of emissions following deforestation and forest degradation, and a potential carbon sink if they can be adequately protected (Gibbs et al., 2007; Malhi et al., 2008). The historically high deforestation rates in Brazilian Amazonia are continuing to fall (INPE, 2011) but estimates of carbon emissions still average 153 TgC $year^{-1}$ (Numata et al., 2011). Despite uncertainty over future international agreements (Venter and Koh, 2012), much hope is still placed in the expansion of bilateral or multilateral Reducing Emissions from Deforestation and Forest Degradation (REDD+) schemes to shift the balance in global markets away from conditions favouring deforestation to those favouring forest protection and biodiversity conservation (Gardner et al., in press).

The effectiveness of such REDD+ policies, implemented by regional and national governments, through mechanisms such as the Amazonian Fund (BNDES, 2010), will require accurate estimation of current carbon stocks within management areas (Salimon et al., 2011), as a pre-requisite to the continuing process of 'Monitoring, Reporting and Verification' (MRV). Protected areas are therefore encouraged to assess their carbon stocks to demonstrate their 'readiness for REDD' (Cerbu et al., 2011; FCPF, 2012). This task is complicated since carbon stocks are far from spatially homogenous, especially within structurally complex tropical forest mosaics (Gibbs et al., 2007), including marked variation across landscapes and forest types (Asner et al., 2010). As a consequence, the large uncertainties in emission estimates (Olander et al., 2008) arise not just from difficulties in tracking the true extent of

* Corresponding author.
E-mail addresses: j.hawes@uea.ac.uk (J.E. Hawes), c.peres@uea.ac.uk (C.A. Peres), louisebryony@hotmail.co.uk (L.B. Riley), lola@eri.ucsb.edu (L.L. Hess).

0378-1127/$ - see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2012.06.023

deforestation and forest degradation, but also from knowledge of the spatial distribution of forest types, including wetland forests (Melack and Hess, 2010), and their respective biomass levels (Achard et al., 2004; Melack and Hess, 2010).

Levels of aboveground biomass (hereafter, AGB) are usually assessed using a combination of remote and field-based measurements (Stickler et al., 2009), the latter of which remain essential to high-resolution verification of the assumptions behind remotely sensed indicators over large spatial scales (e.g. Keith et al., 2009) despite recent advances in high resolution LiDAR technology (Asner et al., 2010). Field-based measurements have the advantages of being low-tech, easily understood, and relatively inexpensive with the principal cost comprising field labour (Gibbs et al., 2007). They have, however, several potential sources of error, including variation in plot sizes and the allometric equations used (Chave et al., 2004). In addition, current estimates of AGB and carbon stocks in tropical forests (Malhi et al., 2006; Saatchi et al., 2007) are still based on extrapolations from a limited number of field sites (Houghton, 2005; Houghton et al., 2009), leaving many regions and forest types underrepresented.

Floodplain forests are one of the most undersampled forest types and their contribution to regional and global scale carbon stocks remains highly uncertain (Anderson et al., 2009), even though wetlands comprise 17% of Central Amazonia (Hess et al., 2003). The most extensive of seven wetland types identified across Amazonia (Pires and Prance, 1985) are *várzea* forests, defined as the white-water floodplains of the Amazon (=Solimões) river and its tributaries (Prance, 1979), and accounting for >200,000 km^2 within Brazilian Amazonia alone (Junk, 1997). The 'white-water' of these rivers is derived from their high load (100 mg l^{-1}) of Andean alluvial sediments (Irion et al., 1997); 300–1000 mm of nutrient-rich deposits (Parolin, 2009) can be added to the soil every year during the annual invasion of floodwaters into the adjacent *várzea* (Sioli, 1984). This cyclic land renewal results in high fertility, and productivity levels two to three times higher than in adjacent *terra firme* forests (Worbes, 1997).

The flooding of the *várzea* lasts for up to 210 days per year, rising to a depth of 10–15 m (Parolin et al., 2004a). This extended period of submersion and waterlogging has severe impacts, notably in oxygen deficiency (Parolin, 2009), reduced photosynthesis from low light penetration through water and mud deposited on leaves, and low water conductance which can paradoxically result in water deficits in the tree crown (Parolin et al., 2004a). Flooding is typically a more frequent source of mortality in trees than desiccation, but the environmental harshness of the *várzea* is compounded by the contrasting drought conditions also experienced when the floods retreat (Parolin et al., 2010). Despite the marked seasonality of *várzea* forests, the annual regularity of the 'flood pulse' (Junk et al., 1989), which drives the timing of many ecological processes within the *várzea*, has operated as a stable selective agent for the evolution of a variety of mechanisms in both adult trees and seedlings to cope with the dramatic annual transition between severe inundation and severe drought (Parolin et al., 2004b; Ferreira et al., 2010; Junk et al., 1989; Worbes et al., 1992; Wittmann et al., 2002).

Such extreme conditions within *várzea* forests may partly explain our poor current understanding of their forest structure (Table 1) but also raise questions over extrapolations in AGB estimates from other forest types, even when in close proximity. Indeed, trees in *várzea* forests display a range of phenological, physiological, and structural adaptations to the annual flood pulse (Parolin et al., 2004b), and many life-history traits are strongly influential on AGB estimates. For example, the hyper-abundant nutrient conditions in the disturbance-prone *várzea* environment favours fast life-histories of short-lived individuals with rapid growth rates, frequently resulting in low wood densities (Fearnside, 1997; Baker et al., 2004b). In addition, unstable soils coupled with the persistent flood pulse promote high rates of tree-falls and canopy fracture, reducing competition for light, and substantially lowering the canopy stature in comparison to *terra firme* forests (Souza and Martins, 2005). Such differences in wood density and tree height suggest that AGB estimates from *terra firme* forests may not be reliably extrapolated across *várzea* plots.

Of the few *várzea* forest inventories available, most are centred around the large urban centres of Tefé, Manaus, and Belém, in the western, central and eastern Brazilian Amazon, respectively. More generally, the small areas of *várzea* sampled to date throughout Amazonia are unlikely to be representative, with vast regions remaining entirely unknown (Parolin et al., 2004a). We are aware of only two *várzea* studies within the vast tracts of forest between existing plot-scale inventories in central Brazilian Amazonia and those in the upper Ecuadorian, Bolivian and Peruvian Amazon (see Saatchi et al., 2007), both along the upper Juruá river: Rodrigues Alves, Acre (Campbell et al., 1992) and Eirunepé, Amazonas (Peres & Malcolm, unpublished data). This study in the remote central Juruá region begins to redress this regional imbalance using a highly dispersed arrangement of small 0.1-ha plots to assess variation in forest structure over a large landscape mosaic, in contrast to the traditional approach of sampling a single or few larger plots.

The study landscape also provides the ideal opportunity to examine differences between *terra firme* and *várzea* forests, which diverge markedly in environmental gradients and life-history traits, and yet typically occur side-by-side. The marked flood regime is expected to drive differences in forest structure and biomass between flooded and unflooded forests but water stress is also likely to have an effect within each forest type, particularly within *várzea* forests. However, environmental stressors may affect plant physiology in different ways across these two forest types. Higher elevation corresponds to increased water shortages in *terra firme* forest but to less severe hydrological stress in *várzea* forests. Conversely, lower elevation may reduce root depth to the water-table and seasonal hydrological deficit in *terra firme* forests but extends the periods of anoxia resulting from water-logging and inundation in *várzea*. We therefore tested the *a priori* hypotheses that AGB is (1) lower in *várzea* than in *terra firme* forest; and (2) negatively related to water stress (i.e. water scarcity in *terra firme*, but water surplus in *várzea*) and to a greater degree in *várzea* than in *terra firme* forest. To fully understand the distribution of AGB in forests with a long history of human occupation it is necessary to examine not only environmental variables related to water stress but also accessibility variables potentially related to logging, which was historically more common in *várzea* than in *terra firme* forests (Scelza, 2008). We therefore examine the additional hypothesis that (3) AGB is negatively related to accessibility (e.g. greater distances from the nearest local community), and to a greater degree in *várzea* than in *terra firme* forest. Finally, we use our findings to provide AGB estimates for two large Amazonian protected areas consisting of both *terra firme* and *várzea* forest, with existing or proposed REDD+ schemes involving payments for forest ecosystem services (Newton et al., 2012a).

2. Methods

2.1. Study area

This study was conducted in the state of Amazonas, Brazil, within two contiguous sustainable use reserves, namely the Médio Juruá Extractive Reserve (*ResEx Médio Juruá*, 253,227 ha) and the Uacari Sustainable Development Reserve (*RDS Uacari*, 632,949 ha) (Fig. 1). The two reserves border the Juruá river, a major white-water tributary of the Solimões (=Amazon) river, and contain large